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# *Typha latifolia* and *Cladium jamaicense* litter decay in response to exogenous nutrient enrichment

R. Corstanje [a,*], K.R. Reddy [a], K.M. Portier [b]

[a] *Wetland Biogeochemistry Laboratory, Soil and Water Science Department, University of Florida, Institute of Food and Agricultural Sciences, 106 Newell Hall, P.O. Box 110510, Gainesville, FL 32611-0510, USA*
[b] *Department of Statistics, 522 McCarty Hall C, P.O. Box 110339, University of Florida, Gainesville, FL 32611-0339, USA*

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**Abstract**

The role of nutrient availability in the decay of *Typha latifolia* and *Cladium jamaicense* litter and associated microbial responses were studied under controlled experimental conditions. The experimental setup consisted of three 14 $m^2$ mesocosms: (i) an experimentally enriched (N&P) mesocosm containing organic soil, (ii) a mesocosm with organic soil but no external enrichment, and (iii) a mesocosm with no external nutrient inputs and a mineral soil, each equally divided into two areas predominated by *T. latifolia* and *C. jamaicense*. Air dried senesced material of each plant species from the three units were placed in litterbags and were introduced back into their respective communities on the soil and water interface. Litter from *T. latifolia* degraded significantly faster than that of *C. jamaicense*. The half life of *T. latifolia* litter averaged approximately 274 days, *C. jamaicense* litter half life was extrapolated to approximately 377 days. Nutrient enrichment significantly increased the decay rates of *T. latifolia*, the nutrient effect on *C. jamaicense* decomposition was less apparent. The microbial biomass carbon in *T. latifolia* and *C. jamaicense* litter increased significantly as the litter decomposed. No significant differences between the litter types or amongst mesocosms were found. The relative activities of the extracellular enzymes acid phosphatase and β-glucosidase were significantly ($P < 0.001$ and $P = 0.0284$, respectively) affected by litter type and mesocosm over time. Litter associated alkaline phosphatase activity was largest in the mineral mesocosm, followed by the organic control and then organic enriched irrespective of litter type, β-glucosidase activity showed an inverse effect, enriched organic > organic control > mineral. The litter $CO_2$ and $CH_4$ microbial production rates showed a significant litter type and mesocosm effect ($P = 0.0003$ and 0.001, respectively). *T. latifolia* litter had larger associated methanogenic and microbial respiration rates than *C. jamaicense* litter. Nutrient enrichment enhanced both forms of microbial metabolic activities ($CO_2$ and $CH_4$ production). The effect of nutrient enrichment was primarily evident in the initial (3–6 months) period of decay, extracellular enzyme activities and the litter associated microbial metabolic activities showed most response during this decay stage.


*Keywords:* Litter decomposition; Eutrophication; *Typha latifolia*; *Cladium jamaicense*; Microbially mediated decomposition; Extracellular enzyme

## 1. Introduction

Wetlands have often been described as detritus based systems, in which most of the carbon (C) and energy is derived from litter (Odum and Heald, 1972). In many wetlands, emergent macrophytes often constitute a major portion of the primary productivity (Wetzel and Howe, 1999), yet only a small percentage of the aboveground biomass is consumed by herbivores (Valiela et al., 1985). As a result, most of this organic C is degraded by the microbial consortia on the detrital vegetation after senescence (Kuehn et al., 1999, 2000) and upon deposition onto the soil surface (DeBusk and Reddy, 1998; Newman et al., 2001). Understanding nutrient and energy flows in wetland systems is therefore intricately linked to the fate of detritus in these systems.

The process of detrital matter decomposition in wetlands and aquatic systems is often distinguished into three phases: (1) leaching of the soluble component, (2) microbial degradation of detrital material, and (3) the physical and biological fragmentation (Valiela et al., 1985). The leaching phase is characterized by a rapid loss of soluble organic compounds (sugars, organic acids, proteins, phenolics, etc.) and minerals (K, Ca, Mg, Mn). This phase can last between a few days to a few weeks (Davis et al., 2003). The second and third phases of decomposition are enhanced by physical and biological

* Corresponding author. Tel.: +1 352 393 1804; fax: +1 352 392 3399.
*E-mail address:* Corstanje@mail.ifas.ufl.edu (R. Corstanje).

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fragmentation of the litter (Harrison and Mann, 1975). Since refractory compounds are what primarily remain after the initial leaching, the secondary and tertiary phases of decomposition take longer, with increasing microbial biomass on the detritus complex. The degradation of plant material is mediated by extracellular enzymes (Chróst, 1991) and models have been developed associating extracellular enzymes to litter mass loss rates (Sinsabaugh and Moorhead, 1994). The secondary and tertiary phases result in a gradual increase in residual nitrogen (N) and phosphorus (P) relative to C, an effect encountered consistently across aquatic systems (Jordan et al., 1989; Davis, 1991; Villar et al., 2001).

The effect of exogenous nutrients in a wetland system could result in the long-term accumulation of these nutrients into the litter material (Davis et al., 2003). The microbial communities involved in decomposition of litter alternatively mineralize or immobilize nutrients during the process (Jordan et al., 1989). Depending on the quality of the litter material, decomposition rates have been found to be both stimulated and not stimulated by N or P additions (Howard-Williams et al., 1988; Jordan et al., 1989; Villar et al., 2001) indicating that nutrient availability is not always a limiting factor for decomposition. In a study by Godshalk and Wetzel (1978), the primary decay rates were a function of the litter C:N ratio, where larger C:N ratios in the litter resulted in lower degradation rates. In a complementary study, Lee and Bukaveckas (2002) compared *Typha latifolia* litter degradation across a variety of wetland systems and found that exogenous P availability to be a useful predictor of decomposition. In essence, depending on the C:N ratio, litter may function as a nutrient sink (nutrient immobilization; Jordan et al., 1989) as the litter is relatively rich in C and poor in N or P. As decomposition continues, utilization of C results in a gradual shift to mineralization over immobilization and litter can become a source of nutrients. Litter degradation rates also respond to the general environment, and thus the addition of P to a P-limited system results in increased decomposition (Qualls and Richardson, 2000). This interaction between the external milieu and internal litter dynamics probably results in some of the uncertainty as to the sensitivity of overall response of litter to the external environment. As such, the objectives of our study were: (1) to evaluate the interaction between internal litter composition (litter source) and the external nutrient loading and (2) to relate microbial biomass community size and activity and associated extracellular enzyme activities to litter degradation.

## 2. Materials and methods

The mesocosms were three 13 m long by 1 m wide raceways located on the University of Florida campus. Two of the mesocosms contained an organic soil and one a mineral soil, the prevalent soil characteristics can be found in Table 1. Each mesocosm was divided into two subsections and were planted with *T. latifolia* on one side of the mesocosm and *Cladium jamaicense* on the other end of the mesocosm. Water levels in all mesocosms were maintained at 45–50 cm depth over the soil surface. One of the organic mesocosms was randomly selected and pulse loaded weekly to attain a loading rate 2 g N $m^{-2}$ $y^{-1}$ ($NH_4Cl$) and 1 g P $m^{-2}$ $y^{-1}$ ($KH_2PO_4$). Although gross scale changes in the soil did not occur as a result of the nutrient enrichment, the continual nutrient addition resulted in the enrichment of primarily the labile and mineralizable P and N fractions (Corstanje, 2003), generating three distinct environments, a comparison between; (i) a system that was significantly nutrient limiting (mineral soil system) as was reflected in the overall nutrient contents and in the related

Table 1
Soil physico-chemical characterization across all three mesocosm at the termination of the experiment

| Mesocosm | Vegetation | Depth (cm) | TP (mg $kg^{-1}$) | TN (g $kg^{-1}$) | TC (g $kg^{-1}$) |
|---|---|---|---|---|---|
| Organic soil-enriched | *T. latifolia* | Detrital | 1189 (172) | 20 (3.3) | 512 (13) |
| | | 0–5 | 571 (33) | 22 (0.7) | 443 (18) |
| | | 5–10 | 342 (39) | 16 (3.1) | 424 (14) |
| | *C. jamaicense* | Detrital | 592 (190) | 12 (0.8) | 439 (38) |
| | | 0–5 | 391 (53) | 14 (4.5) | 402 (36) |
| | | 5–10 | 357 (98) | 33 (2.7) | 418 (29) |
| Organic soil-control | *T. latifolia* | Detrital | 1206 (110) | 20 (1.5) | 444 (45) |
| | | 0–5 | 599 (259) | 17 (3.9) | 396 (48) |
| | | 5–10 | 285 (105) | 15 (2.2) | 391 (47) |
| | *C. jamaicense* | Detrital | 689 (76) | 13 (2.1) | 457 (34) |
| | | 0–5 | 453 (39) | 16 (1.4) | 438 (22) |
| | | 5–10 | 289 (1) | 13 (6.4) | 455 (0.1) |
| Mineral soil | *T. latifolia* | Detrital | 948 (417) | 28 (2.4) | 426 (39) |
| | | 0–5 | 337 (377) | 6 (10) | 158 (28) |
| | | 5–10 | 27 (23) | 0.13 (0.19) | 5 (3.3) |
| | *C. jamaicense* | Detrital | 441 (313) | 10 (4.3) | 433 (10) |
| | | 0–5 | 143 (120) | 7 (11) | 233 (56) |
| | | 5–10 | 28 (48) | 0.27 (0.2) | 30 (16) |

TP, total phosphorus; TN, total nitrogen; TC, total carbon; the values denote means and S.D. are in brackets, $n = 3$.

Table 2
Initial physico-chemical litter characteristics

| | *T. latifolia* | *C. jamaicense* |
|---|---|---|
| ASDM ash content (%) | 2 | 2 |
| TC (g $kg^{-1}$) | 462 | 441 |
| TN (g $kg^{-1}$) | 6.6 | 5.1 |
| TP (mg $kg^{-1}$) | 256 | 209 |

ASDM, ash-free dry mass; TC, total carbon; TN, total nitrogen; TP, total phosphorus.

microbial activities (Corstanje, 2003), (ii) a system that was not significantly nutrient limited, in which in the soil nutrient contents are similar to freshwater marsh systems with similar macrophyte composition, and (iii) a system that was recipient of a continual nutrient influx with changing soil nutrient status.

Plant litter material was collected from all three mesocosms prior to loading. The litter material consisted of air-dried senesced standing dead leaves from *Typha* and *C. jamaicense*, respectively, the litter physico-chemical characteristics can be found in Table 2. Equal amount of litter material from the three mesocosms was cut into 5 cm pieces and thoroughly mixed, keeping only the plant source (*T. latifolia* or *C. jamaicense*) separate. Litterbags were made by weighing 15 g of the material into 2 mm fiberglass widow screening. The mesh-size of the litterbags was identified by Bradford et al. (2002) as a mesh diameter that allows for micro- and meso-fauna (excluding primary worms, slugs and insect larvae). The litterbags were placed back in the mesocosms, with the bags containing *T. latifolia* placed in mesocosm sections where *T. latifolia* was the dominant macrophyte community and likewise the *C. jamaicense* bags were placed in *C. jamaicense* areas. The litterbags were placed underwater, on the soil surface in the mesocosms and remained submerged until collection. The litterbags were divided evenly and distributed randomly over three areas within the plant communities, each area extending 1.5 $m^2$ and separated by 1 m.

The litterbag experiment lasted 1 year and sampled quarterly. A minimum of three litterbags (one per area) were collected per vegetation type per mesocosm on each sampling event (a total of 18 per sampling event). Upon collection, attached soil, detritus and any live roots were removed from the bags. The bags were weighed and a subsample was dried at 70 °C and subsequently ashed at 550 °C to obtain the ash free dry matter (AFDM) to determine plant litter weight loss and litter nutrient content.

Total carbon (TC) and total nitrogen (TN) were determined on oven dried, ground samples with a Carlo-Erba NA 1500 CNS Analyzer (Haak-Buchler Instruments, Saddlebrook, NJ). Total phosphorus (TP) was determined on the same oven dried ground sample by the TP ashing method (Andersen, 1976) and analyzed by the ascorbic acid colorimetric procedure (Kuo, 1996; Technicon Autoanalyzer II; Terrytown, NY). Anaerobic respiration was determined on the litter material using 5 g of sample with 10 mL of deionized distilled (DDI) water in 27 mL anaerobic tubes (Bellco Glass, Vineland, NJ). The litter slurry was subsequently actively purged with $O_2$-free $N_2$ after the anaerobic tubes were capped with butyl stoppers-aluminum crimps (Wheaton, Millville, NJ). Upon completion of a 2 week preincubation, the headspace was purged again with $O_2$-free $N_2$ and $CO_2$ and $CH_4$ headspace content monitored over a period of 4 days. Headspace $CO_2$ was measured through thermal conductivity detector (Shimadzu 8AIT GC) and headspace $CH_4$ was analyzed by means of flame ionization detection (Shimadzu 8AIF GC).

The microbial biomass carbon (MBC) associated to the litter was determined by a chloroform fumigation incubation procedure with a subsequent 0.5 M $K_2SO_4$ extraction (Vance et al., 1987). The MBC was computed as the difference in the dissolved organic C from a treated (fumigated) and untreated sample, corrected with an extraction efficiency factor $k_{EC} = 0.37$ (Sparling et al., 1990). The dissolved organic C (DOC) in the $K_2SO_4$ extractant was determined on a Shimadzu total organic carbon analyzer (TOC-5050A). Fluorescent artificial substrate methyl-umbelliferone (MUF-phosphate and MUF-β-D-glucoside, respectively) was used to determine the extracellular enzyme (EE) activities of β-1,4-glucosidase (βGA; EC 3.2.1.21) and acid phosphatase (APA; EC 3.1.3.1) on 96-well microtiter plates. Enzyme activity was expressed as the mean difference in fluorescence reading (Bio-Tek FL600 fluorometric plate reader, Bio-Tek Instruments Inc.) between the blank and sample over the incubation period (Prenger and Reddy, 2004).

## 3. Decay model and data analysis

Preliminary analysis indicated that the litter mass loss responses were nonlinear, as result the litter decomposition rates were modeled using the following equation (Godshalk and Wetzel, 1978):

$$W_t = W_o \exp[(k_1/k_2)(\exp(-k_2 t) - 1)]$$

where $W_o$ is the original amount of litter material, $W_t$ the amount of litter material at time $t$, and $k$, $k_1$ and $k_2$ are estimated kinetic parameters. The relative magnitude of the coefficients $k_1$ and $k_2$ determine the shape of the decay curve, and $k_1$ is associated to the overall decay rates of the material whereas $k_2$, as a function of $k_1$, is an indication of the increasing recalcitrance of the material. Kinetic parameters were estimated using nonlinear models (nonlinear regression procedure; NLIN, SAS version 8.0.2). Unless otherwise noted, statistical significance was tested at the $\alpha = 0.05$ level. Analysis of covariance (ANCOVA) was used to test for differences in the decay rates, chemical concentrations and the related microbial activities.

## 4. Results

The decaying coefficient model applied to the litter mass loss resulted in an overall good coefficient of determination ($r^2 > 0.9$). Over the three different mesocosms, the highest mass loss rates were associated with the litter in the enriched soil mesocosm (Table 3), followed by the organic mesocosm and finally the mineral soil mesocosm irrespective of plant species. *T. latifolia* plant litter degraded significantly faster than *C. jamaicense* litter ($P < 0.001$), across all mesocosms, no

Table 3
Kinetic analysis of litter mass decomposition of *T. latifolia* and *C. jamaicense* in three mesocosm

| Macrophyte | Mesocosm | $k_1$ ($y^{-1}$) | $k_2$ ($y^{-1}$) |
|---|---|---|---|
| *T. latifolia* | Organic soil-enriched | 1.7 (0.1) | 1.6 (0.2) |
| | Organic soil-control | 1.1 (0.06) | 0.38 (0.2) |
| | Mineral soil | 0.81 (0.08) | 0.19 (0.3) |
| *C. jamaicense* | Organic soil-enriched | 0.95 (0.06) | 0.98 (0.2) |
| | Organic soil-control | 0.98 (0.06) | 1.56 (0.2) |
| | Mineral soil | 0.38 (0.06) | −0.64 (0.3) |

The values denote the estimated coefficients; the numbers in the brackets are the associated S.E. estimates.

significant litter and mesocosm interaction was noted. Half life of *T. latifolia* litter decay in other ecosystems was reported to be approximately 300 days or more (Morris and Lajtha, 1986; Schnitzer and Neely, 2000). In the current study, the half life of *T. latifolia* litter averaged approximately 274 days. The half life of the *C. jamaicense* litter was extrapolated to approximately 377 days. Total litter C decreased throughout the experiment (Fig. 1), with no significant differences between the mesocosms or litter types. Litter C content remained fairly constant throughout the experiment (Fig. 1). The profiles of N accumulation were similar in all mesocosms (Fig. 2), total levels of N decreased initially (<100 days), after which they stabilized or increased slightly in some cases. The increases in N content *T. latifolia* were significantly larger than the N content increases in *C. jamaicenses*. In this study, increasing the levels of P has resulted to P enrichment of the litter during the decomposition process (enriched mesocosm, Fig. 3). The enrichment of P content and increases in total P in *C. jamaicense* showed more variability than the corresponding increases in P in *T. latifolia*. Litter P content varied little between the organic control and inorganic mesocosms and generally showed a slight decrease.

The APA activities did not vary considerably across the experimental period and showed no significant difference between the litter type source (Fig. 4), responding primarily to the environment in which the litter was placed ($P < 0.001$). The litter in the mesocosm with the mineral soil consistently exhibited the highest APA activity, followed by that of the control. The APA activities in the enriched mesocosm were

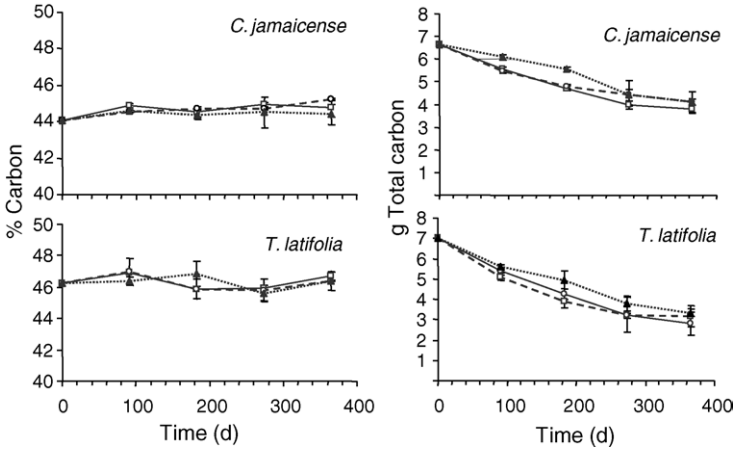


Fig. 1. Total C in the litterbag and litter C content of *T. latifolia* and *C. jamaicense* over the experimental period over the three mesocosms (▲, mineral mesocosm; □, organic soil-enriched; ○, organic soil-control; the error bars denote S.D.).

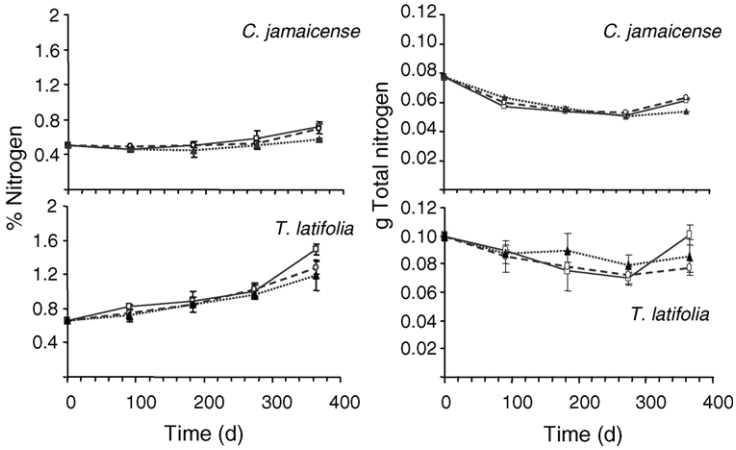


Fig. 2. Total N in the litterbag and litter N content of *T. latifolia* and *C. jamaicense* over the experimental period over the three mesocosms (▲, mineral soil; □, organic soil-enriched; ○, organic soil-control; the error bars denote S.D.).

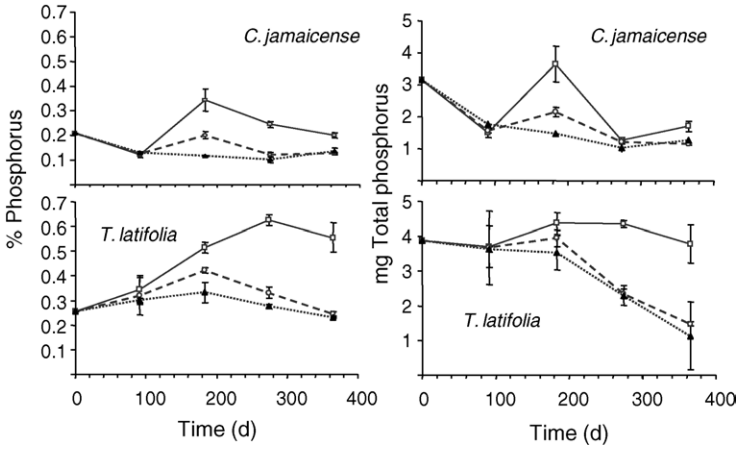


Fig. 3. Total P in the litterbag and litter P content of *T. latifolia* and *C. jamaicense* over the experimental period over the three mesocosms (▲, mineral soil; □, organic soil-enriched; ○, organic soil-control).

relatively lower to those in the two control mesocosms. The βGA decreased significantly during the course of the experiment (Fig. 4). Although not consistently across the two litter types and three mesocosms, βGA activity leveled off 6 months into the decay process. The litter in the enriched mesocosm exhibited significantly larger βGA values than that in the organic control, which in turn, was significantly larger than the βGA values in the mineral mesocosm. The βGA levels varied across the specific litter type (*T. latifolia* or *C. jamaicense*) and by mesocosm ($P = 0.0284$), indicating that the combination of external nutrient conditions and internal litter quality significantly effects the βGA enzyme activity over time.

The biomass associated with *T. latifolia* and *C. jamaicense* litter increased significantly over the experimental period (Fig. 5) with no significant differences between the litter types or amongst mesocosms. The overall proportion of MBC to litter TC increased over the course of the experiment from about 3 % (±0.1%) to 6% (±0.2%). Whilst there was an overall increase in biomass, the associated microbial activities decreased over the experimental period, both for the methanogenic activities and the $CO_2$ production (Fig. 6). The microbial activities (Fig. 6) associated to the litter decay showed responses to both the increase of external nutrients and litter type, in both cases the interaction of mesocosm and litter type was significant ($P = 0.0003$ for $CO_2$ production rates and $P = 0.001$ for the potential methanogenesis). *T. latifolia* litter in the enriched mesocosm generated the highest overall microbial activities, followed by the organic, and finally the mineral mesocosm; the microbial activity associated to *C. jamaicense* was consistently lower than that associated with *T. latifolia* and showed a similar decrease in activity from the enriched, control to mineral mesocosm.

## 5. Discussion

Comparable decay coefficients for the decaying coefficient model were not available as the model has been sparsely applied throughout the literature. Rapidly decomposing species resulted in high $k_1$ values (Godshalk and Wetzel, 1978); the $k_1$ values in the organic enriched and control mesocosms indicated fairly rapid decomposition rates, slower rates were found in the

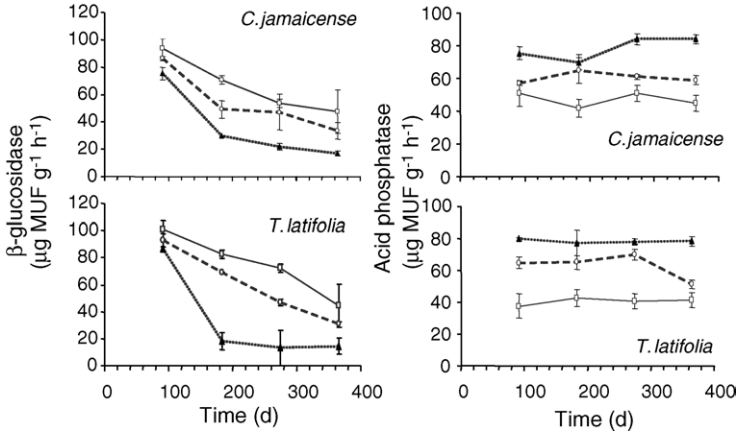


Fig. 4. Extracellular enzyme activity levels associated with *T. latifolia* and *C. jamaicense* (▲, mineral soil; □, organic soil-enriched; ○, organic soil-control; the error bars denote S.D.).

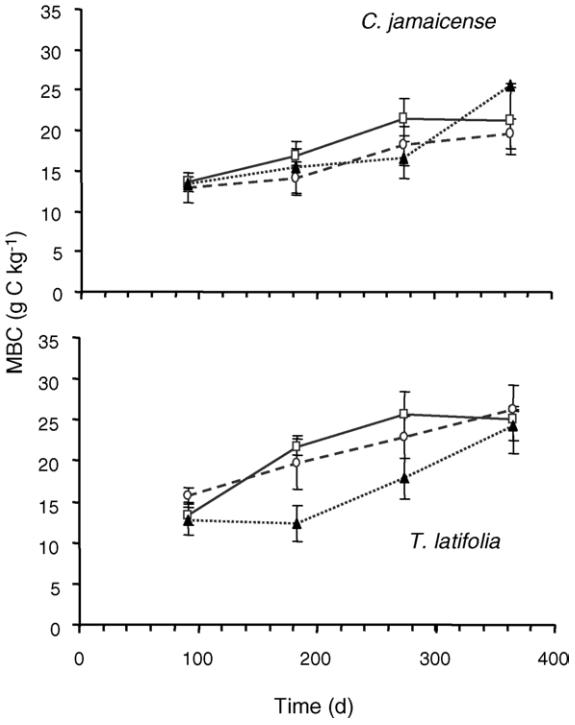


Fig. 5. Microbial biomass (MBC) associated with of *T. latifolia* and *C. jamaicense* over the experimental period over the three mesocosms (▲, mineral soil; □, organic soil-enriched; ○, organic soil-control; the error bars denote S.D.).

mineral mesocosms. Interpretation of the $k_2$ values could only be done in association with the corresponding $k_1$. High $k_1$ values such as those obtained in the organic soil mesocosms associated with high $k_2$ indicate high initial decay rates and moderate rates of continued loss. We found this to be the case for the nutrient loaded mesocosm and for *C. jamaicense* litter in the organic control. High $k_1$ values associated with low $k_2$ values indicate high initial decay rates with continual high rates of mass loss, which was the case for *T. latifolia* in the organic control. The decay rates in the mineral soils have both low $k_1$ and $k_2$ values, which indicated a relatively uniform decay process throughout the experimental period (Godshalk and Wetzel, 1978).

The general response of litter degradation to external nutrient levels is mixed, Howard-Williams et al. (1988), Jordan et al. (1989) and Villar et al. (2001) showed no effect, suggesting that litter degradation is primarily regulated through internal nutrient dynamics (litter C:N, C:P and N:P ratios). Lee and Bukaveckas (2002) contrasted the degradation rates of standardized *T. latifolia* across a number ($n = 10$) of wetland systems and the water and soil nutrient content were significant predictors of decomposition rates. They postulated that across systems, the nutrient levels in the environment were as important as the nutrient content of litter in controlling litter degradation. In our study, the largest differences in litter decomposition were seen between litter types, with *C. jamaicense* degrading at overall slower rates than *T. latifolia*. However, the overall decay rates of both litter types differed significantly between the mesocosms, indicating that both litter types as well as nutrient loading can have significant effect on litter degradation.

Decay rates of different macrophytes are correlated with the total amount of fiber constituents present in the tissue, which, in turn, is correlated with the C:N ratio (Lee and Bukaveckas, 2002). At mass ratios of C:N < 30 and C:P < 200, net mineralization of N and P are likely to occur under aerobic conditions (Fenchel et al., 1998) and the overall decay process will be slower. The initial C:N and C:P ratios found for this material (Table 4) would not suggest that mineralization of organic P and N will control the C loss rates during the decomposition process.

As decomposition ensues, the relative enrichment of nutrients (N and P) in the material results in corresponding decreases in litter C:N, C:P and N:P ratios (Kuehn et al., 1999; Table 4). During decomposition, the N and P content in the litter often decreases initially (Kuehn et al., 1999) as it leaches from the tissue. This period is therefore similar in size to that associated with the ''leaching phase'' of the litter degradation (1–2 months). Ensuing this initial period of loss, the material is selectively enriched in N and P, as C is continually lost (Kuehn et al., 1999, 2000; Newman et al., 2001; Villar et al., 2001; Davis et al., 2003). Furthermore, microbial colonization of the litter material can result in immobilization of N and P into their

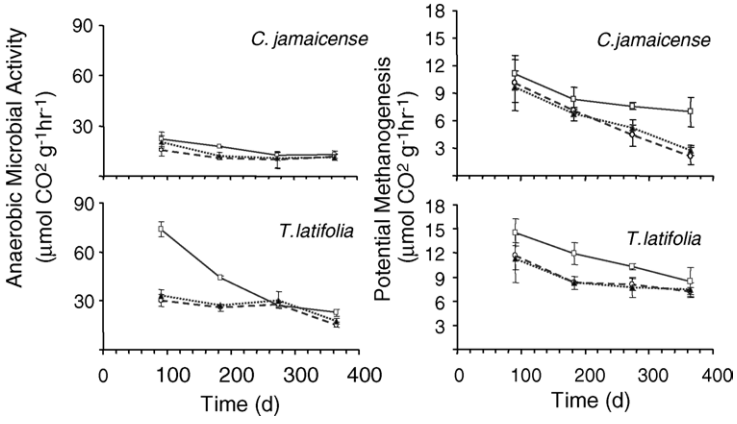


Fig. 6. Anaerobic basal respiration and potential methanogenesis of *T. latifolia* and *C. jamaicense* litter in the three mesocosms (▲, mineral soil; □, organic soil-enriched; ○, organic soil-control; the error bars denote S.D.).

Table 4
C:P, C:N, and N:P ratios (by weight) of *T. latifolia* and *C. jamaicense* litter decay under submerged conditions in three mesocosms, one containing mineral soil and two organic soils, one of the organic soil mesocosms was enriched with nutrients

| Macrophyte | Mesocosm | Month | C:N | C:P | N:P |
|---|---|---|---|---|---|
| *T. latifolia* | Organic soil-enriched | 0 | 70 | 1805 | 26 |
| | | 3 | 46 (2) | 736 (13) | 16 (0.4) |
| | | 6 | 57 (0.8) | 1396 (148) | 25 (3) |
| | | 9 | 31 (0.9) | 847 (51) | 27 (1) |
| | | 12 | 53 (3) | 892 (21) | 17 (2) |
| | Organic soil-control | 0 | 70 | 1805 | 26 |
| | | 3 | 45 (2) | 1384 (56) | 31 (1) |
| | | 6 | 63 (5) | 1524 (179) | 24 (3) |
| | | 9 | 36 (1) | 1900 (50) | 52 (2) |
| | | 12 | 54 (0.3) | 1085 (18) | 20 (0.2) |
| | Mineral soil | 0 | 70 | 1805 | 26 |
| | | 3 | 48 (2) | 1652 (23) | 35 (1) |
| | | 6 | 64 (3) | 1544 (34) | 24 (1) |
| | | 9 | 39 (3) | 1995 (11) | 47 (0.4) |
| | | 12 | 56 (4) | 1420 (102) | 25 (0.8) |
| *C. jamaicense* | Organic soil-enriched | 0 | 86 | 2107 | 24 |
| | | 3 | 79 (7) | 3126 (153) | 40 (3) |
| | | 6 | 97 (2) | 3731 (165) | 38 (2) |
| | | 9 | 62 (2) | 2229 (65) | 36 (2) |
| | | 12 | 89 (4) | 1211 (103) | 15 (2) |
| | Organic soil-control | 0 | 86 | 2107 | 24 |
| | | 3 | 84 (5) | 3669 (181) | 44 (4) |
| | | 6 | 91 (0.7) | 3517 (28) | 39 (0.6) |
| | | 9 | 66 (3) | 3559 (93) | 54 (1.3) |
| | | 12 | 89 (2) | 2229 (87) | 25 (0.7) |
| | Mineral soil | 0 | 86 | 2107 | 24 |
| | | 3 | 88 (3) | 4384 (319) | 50 (3) |
| | | 6 | 96 (3) | 3436 (73) | 36 (2) |
| | | 9 | 77 (1) | 3257 (159) | 42 (2) |
| | | 12 | 101 (9) | 3784 (71) | 38 (2) |

Values are means, the numbers in the brackets indicate 1 S.D. ($n = 3$).

tissues, increasing the overall N and P content of the decomposing material. In this study, we noted an increase in N and P relative to the overall mass decreases and associated decrease in C (Figs. 1–3). However, it is unclear what portion of the increase in litter nutrient content can be ascribed to the microbial biomass (Kuehn et al., 2000), and to what degree the progressive enrichment was a result of microbially mediated C mineralization. Further increasing the levels of environmental P has lead, both in this study (enriched mesocosm, Fig. 3) as in a dosing study ($3.2\ g\ m^{-2}\ y^{-1}$) conducted by Newman et al. (2001) to significant P enrichment of the litter during the decomposition process.

A limiting step in the decomposition processes in aquatic systems is the extracellular hydrolysis of the litter material (Meyer-Reil, 1991). Our study monitored the activity of two extracellular enzymes (EE), acid phosphatase activity and β-glucosidase activity. Repression or production of APA by microbial communities has been shown to correspond to the relative availability of P (Chróst, 1991). Production of this EE relative to C-acquiring enzymes, such as βGA gives a gross assessment of prevalent microbial nutrient requirements (Sinsabaugh and Moorhead, 1994). In comparing the relative activities of the litter associated EE activities, the proportion of APA to βGA on the litter in the mineral mesocosm was considerably larger from that both in organic mesocosms. Given that the same litter material was placed in all three mesocosms, the microbial communities in the mineral mesocosms allocate significantly more resources to P-acquisition than the communities present in the organic mesocosms. Future studies should consider a more complete set of EE assays, including N-acquiring enzymes and polyphenol degrading enzymes, such as phenol oxidase, should result in a more comprehensive depiction of the microbial response to the interaction between the internal litter quality and external environmental factors.

A measure of the relative efficiency of the microbial groups is the ratio of basal respiration (anaerobic $CO_2$ production) to microbial biomass (MBC), i.e. the metabolic coefficient $qCO_2$ (Anderson and Domsch, 1990) is. Larger $qCO_2$ values are typically associated with microbial communities that are undergoing some form of sublethal stress that results in a larger portion of the labile C-pool being catabolized to $CO_2$ versus being incorporated into the biomass (Dilly and Munch, 1996). We found that overall $qCO_2$ ratios decreased as litter

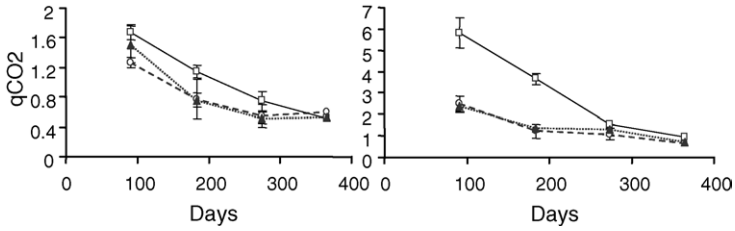


Fig. 7. The metabolic quotient ($qCO_2$) of *T. latifolia* and *C. jamaicense* litter during the course of decomposition in a mineral, organic control and organic enriched unit mesocosms (▲, mineral soil; □, organic soil-enriched; ○, organic soil-control; the error bars denote S.D.).

decomposition progressed (Fig. 7), indicating the presence of microbial communities that were more efficient at using C compounds in later stages of decay. During the first stages of decomposition (<200 days) the $qCO_2$ ratio was significantly larger in the enriched mesocosm than in the other two mesocosms. This divergence in $qCO_2$ ratios gives an indication of the overall effect of environmental factors on the decomposition process in that it enhances the microbial activity and C turnover where the C source is not limiting. After this period, there were no significant differences among the three mesocosms. *C. jamaicense* litter responded in a similar fashion; however, the increase in activity was not statistically significant. Although, a smaller fraction of total anaerobic C turnover, we found that methanogenic microbial activities were very sensitive to nutrient enrichment and litter type. The increased $qCO_2$ values and methane production rates for *T. latifolia* were consistent with the higher decay rates found for this litter type. This was not case for *C. jamaicense*, where the increase in methanogenesis did not correspond with an increase in $qCO_2$ and higher decay rates.

This study and others (Qualls and Richardson, 2000, Newman et al., 2001) illustrate the importance of litter in wetland nutrient dynamics. The litter in the enriched mesocosms selectively accumulated P, immobilizing it from the immediate surroundings. External nutrient influxes into a wetland system would result in an immediate enrichment of existing litter layer. In a number of wetland systems (for e.g. Blue Cypress Marsh, Prenger and Reddy, 2004; Everglades, Davis, 1991) nutrient enrichment has resulted in the incursion of *T. latifolia* in areas historically dominated by *C. jamaicense*. As a result, the litter types are mixed, especially where the *C. jamaicense* stands are in close proximity to *T. latifolia* encroachment. Mixing litter of different types has been noted to have a synergistic effect on the overall decomposition rates (Wardle et al., 1997; Bardgett and Shine, 1999); mixing litter of greater quality can enhance the decomposition rates of other litters (Seastedt, 1984). Whereas our study did not show increased *C. jamaicense* decomposition rates as a function of nutrient enrichment, futures studies might address the effect of mixed litter types on litter decay.

## 6. Conclusions

The kinetic considerations associated to the litter decay rates obtained in this study would confer that litter from *T. latifolia* decays faster than litter from *C. jamaicense*. Furthermore, nutrient enrichment enhances the initial decay rates of *T. latifolia* (high $k_1$) ensued by a slower secondary phase (high $k_2$) whilst the decay rates in the other two mesocosms remained relatively constant throughout the experiment ($k_1 > k_2$). Nutrient enrichment did not affect the decay of *C. jamaicense* in a similar manner as the initial litter decay rates were similar over both organic mesocosms. However, we did find a slower secondary phase for the organic control mesocosm (high $k_1$ and $k_2$). Mesocosm with mineral soils resulted in slower litter decomposition rates for both litter types.

The similarity in the microbial activities and βGA values show that litter quality was an important determinant in microbial activities, in that the more labile components were utilized first and seemed to plateau in 200–300 days into the decay process, possibly as a response to the gradual decrease in the lability of the material. Subsequently, both enzymes and metabolic activities (e.g. $qCO_2$) indicate that the first period of decay (3–6 months) was the most characteristic time bracket in defining differences between the litter type and effect of nutrients on the microbial activities.

*C. jamaicense* did not show as clear a response to nutrient enrichment as *T. latifolia*. The overall cellulose and lignin content of the two species has not been found to be significantly different (DeBusk and Reddy, 1998) so the differences in the decay profiles were presumably due to some other structural component possibly the relative porosity of litter material. Visually, *C. jamaicense* litter was far denser as a material than *T. latifolia*, as a result, the more labile components were less accessible to microbial action than in *T. latifolia* resulting in a more gradual decay rate.

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